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A new species of Megacerini (Cervidae, Artiodactyla) from the Late Miocene of Taralyk-Cher, Tuva (Russia), and remarks on the relationships of the group☆

Une nouvelle espèce de Megacerini (Cervidae, Artiodactyla) dans le Miocène supérieur de Tuva (Russie) et remarques sur les relations phylétiques du groupe

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Abstract

A new species of a megacerine deer, *Praesinomegaceros venustus*, from the Taralyk-Cher locality in the Tuva region on the south of Eastern Siberia, Russia, is described. *P. venustus* nov. sp., the oldest known megacerine, occurred in Asia in the Late Turolian, about 7 Ma. The early history of megacerines is discussed. The existence of the phyletic lineage *Cervavitus-Praesinomegaceros-Sinomegaceros* in Asia is confirmed.

Keywords: Megacerini; *Praesinomegaceros*; Miocene; Asia; Evolution

Résumé

Une nouvelle espèce de cerf mégacérine, *Praesinomegaceros venustus*, dont les restes on été trouvés dans le site de Taralyk-Cher (Tuva, Sibérie Orientale, Russie), est décrite. *P. venustus* nov. sp. est le plus ancien mégacérine connu ; il vivait en Asie au Turolien supérieur (environ 7 Ma). L'évolution et l'origine du groupe sont discutées ; la lignée phylétique asiatique *Cervavitus-Praesinomegaceros-Sinomegaceros* est confirmée.

Mots clés : Megacerini ; *Praesinomegaceros* ; Miocène ; Asie ; Évolution

1. Introduction

Megacerine deers are one of the most impressive and well distinct groups of artiodactyls. Since Viret (1961), their attribution to a separate tribe, Megacerini is widely accepted. Despite a considerable progress in the study of the group achieved in recent time, there are a number of unresolved questions concerning its taxonomy, evolution and phylogeny.

These extinct inhabitants of Eurasia occurred from the Late Miocene to the Holocene and especially flourished in the Middle and Late Pleistocene. The most widely-known of them, the giant deer or ''Irish elk'' *Megaloceros giganteus* (Blumenbach, 1803), with its huge antlers attracts the attention of many researchers. The history of megacerines before the Late Pliocene is less well known mainly because of a poor fossil record. Two Late Miocene genera (*Praesinomegaceros* Vislobokova, 1983 and *Neomegaloceros* Korotkevitsch, 1971) attributed to this group are represented by very scarce remains from Central Eurasia.

Recently, the numerous remains of the most ancient megacerine deer of the genus *Praesinomegaceros* were excavated on the south of Eastern Siberia in the Taralyk-Cher locality, 18 km south to the Kysyl town, by the team of the Paleontological Institute of the Russian Academy of Sciences

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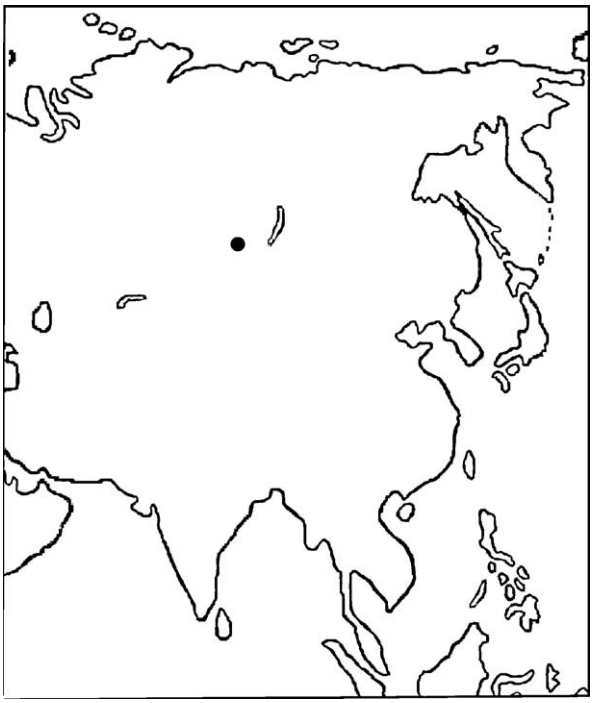

Fig. 1. Location of the Taralyk-Cher locality.

(PIN; Fig. 1). The specimens come from the Late Miocene deposits of the Edygei Formation. The deer were found in association with a dipodid *Heterosmintus saraicus* Zazhigin, Lopatin and Pakatilov, 2002 (determined by A. Lopatin, PIN), the musk deer *Moschus grandaevus* Schlosser, 1924, an odocoileine deer *Pavlodaria* Vislobokova, 1980, and a suine *Chleuastochoerus* Pearson, 1928 (Vislobokova, in press; Vislobokova and Lavrov, 2009). The faunal composition indicates a late Turolian age. The nearest analogues of the Taralyk-Cher fauna appear to be the Olkhon fauna (MN12) from the Sarai Member of the Sasin Sequence in the Olkhon Island, Lake Baikal, and the Pavlodar fauna (Gusinyi Perelet, MN12) in the south of Western Siberia, as well as the Baode fauna in China.

The genus *Praesinomegaceros* was first found in the Upper Miocene (Khirgis-Nur Formation, levels 10–24) of Khirgis-Nur II, Mongolia (Vislobokova, 1983). It was regarded as a predecessor to *Sinomegaceros* Dietrich, 1933 from the Late Pliocene – Pleistocene of Asia (Vislobokova, 1990; Vislobokova and Hu, 1990). We supposed that the origin of the *Praesinomegaceros-Sinomegaceros* lineage was connected with a pliocervine deer of the genus *Cervavitus* Khomenko, 1913.

This paper describes a new species of *Praesinomegaceros* from Taralyk-Cher which differs from the Mongolian species in morphology and distribution, and considers the early history of Asiatic megacerines with a short comment in reference to the whole group and its relationships. New fossil remains of *Praesinomegaceros* from Tuva considerably enlarge the knowledge on morphology of that genus and support our previous hypotheses. With the fossil findings from Tuva, more antler and teeth characters of *Praesinomegaceros* become available. The diagnosis of the genus is refined and enlarged, and new evidences help to clarify the early history of megacerine deer, their origin and relationships, and provide a good basis for further phylogenetic reconstructions.

The described fossil remains are stored at the Paleontological Institute of the Russian Academy of Sciences, Moscow. The dental nomenclature used in the paper is after Heintz (1970) and Gentry et al. (1999) with a minor modification (following Matthew, 1929, the name ‘‘hypocone’’ for the postero-lingual cone of the upper molars is replaced by the metaconule). The measurement system is after Heintz (1970).

2. Systematic paleontology

Order ARTIODACTYLA Owen, 1848
Family CERVIDAE Goldfuss, 1820
Subfamily CERVINAE Goldfuss, 1820
Tribe MEGACERINI Viret, 1961.

Diagnosis: Generally medium- and large-sized. Praeorbital pits small; ethmoidal fissure small or absent; pedicles short, divergent; antlers with flattened, often palmate distal part; brow tine absent or present, being sometimes flattened and palmate; upper canines absent. The mandible is thickened (pachygnathous). *Palaeomeryx* fold in lower molars absent. Robust metacarpals. Plesiometacarpal.

Content: *Megaloceros* Brookes (1827) (=*Megaceros* Owen, 1844), Middle Pleistocene-Holocene, Eurasia; *Praemegaceros* Portis, 1920, Early-Middle Pleistocene, Eurasia; Holocene, Europe; *Praedama* Portis, 1920, Early-Middle Pleistocene, Eurasia; *Sinomegaceros* Dietrich, 1933, Late Pliocene-Pleistocene, Asia; *Arvernoceros* Heintz, 1970, Late Pliocene-Early Pleistocene, Europe; *Neomegaloceros* Korotkevitsch, 1971, Late Miocene, Ukraine; *Candiacervus* Kuss, 1975, Middle-Late Pleistocene, Mediterranean (Crete, Karpathos); *Orchonoceros* Vislobokova, 1979, Late Pliocene, Central Asia; *Praesinomegaceros* Vislobokova, 1983, Late Miocene, Central Asia.

Comparison: Differs from the tribe Cervini in the smaller sizes of the praeorbital pits and ethmoidal fissures, the absence of upper canines, the presence of the pachyostosis in the mandible, and more robust metacarpals.

Remarks: There is no universal opinion regarding the composition of the group. Viret (1961) has proposed the tribe Megacerini for the genus *Megaceros.* This generic name, largely accepted in the last century, was replaced by *Megaloceros* (Lister, 1987; ICZN, 1989).

Some recent researchers include all Pleistocene megacerines in this single genus (Kahlke and Hu, 1957; Lister, 1994; Kahlke, 1999; Pfeiffer, 2002; Lister et al., 2005). However, there is strong evidence that Asian Pleistocene megacerines belong to a separate genus, *Sinomegaceros* (Dietrich, 1933; Shikama and Tsugawa, 1962; Otsuka and Shikama, 1977; Vislobokova, 1990; Van der Made and Tong, 2008). McKenna and Bell (1997) classified them in this way and included up to 12 genera in the tribe Megacerini. Their classification is used here with the exception of four genera: in my opinion, the

genera *Megaceroides* Joleaud, 1914, *Allocaenelaphus* Radulesco and Samson, 1967, and *Nesoleiposeros* Radulesco and Samson, 1967, are synonyms of *Praemegaceros* whereas *Psekupsoceros* Radulesco and Samson, 1967 is a synonym of *Eucladoceros* (Vislobokova, 1990). I recognized the existence of the genera *Praemegaceros* and *Praedama* in the Pleistocene (Vislobokova, 1981, 1990) following Kahlke (1965, 1969, 1971, 1975, 1997). Other students refer *Praedama* to *Megaloceros* (Azzaroli, 1994; Lister, 1994; McKenna and Bell, 1997; Van der Made, 2006; Van der Made and Tong, 2008). Recently, Abbazzi (2004) gave good arguments for the validity of *Praemegaceros*. She also supports *Megaceroides* for the endemic species *M. algericus* (Lydekker, 1890) from the Late Pleistocene of North Africa.

Genus ***Praesinomegaceros*** Vislobokova, 1983

Type species: *P. asiaticus* Vislobokova, 1983, Upper Miocene, Mongolia, Khirgis-Nur II.

Revised diagnosis: Medium-sized. Frontals slightly concave on either side of the interfrontal suture in front of the pedicles; between the pedicles, they are flattened. Pedicles short and almost in the forehead plane, widely spaced, with largest anteroposterior diameter. Antlers short and flattened. Large, tubercle-like burr. Beam short, stout, weakly inclined backwards from the burr and curved upwards below the second bifurcation. Brow tine inserted close to the burr, long, directed upward, forward and outward and strongly flattened transversally. A small accessory point (tine) is present on the brow tine or at the first bifurcation between the main beam and brow tine. Second fork not very far from the first bifurcation. Moderate pachyostosis in the mandible. Premolar row relatively long. Weak molarization of lower p4 metaconid slightly enlarged but not fused with the paraconid. Weak entostyle and cingulum in the upper molars. Facets for proximal ends of Mc II and Mc V on the cannon bone present.

Content: Two species: *P. asiaticus* Vislobokova, 1983 and *P. venustus* nov. sp.

Comparison: Differs from other genera of the tribe Megacerini in its smaller size and shorter and less divergent antlers and from all of them except *Praedama* in the probable absence of the distal palmation in the antlers; from *Sinomegaceros* in a weaker backward inclination of the beam, a lesser expansion (palmation) of the brow tine and its anteroposterior orientation, the possible presence of the accessory points at the first bifurcation and on the brow tine, a weaker pachyostosis in the mandible, and a more elongated premolar row; from *Arvernoceros* in a shorter and more flattened beam, a more elongated and expanded brow tine, and the weaker developed entostyle and cingulum in the upper molars.

Distribution: Late Miocene (Turolian, MN12-13), Mongolia and Russia.

Praesinomegaceros venustus Vislobokova nov. sp.

Holotype: A partial skull roof with nearly complete right antler, PIN 5126/1; Taralyk-Cher, Russia.

Etymology: From *venustus* (lat. = graceful, refined).

Hypodigme: Several portions of the antlers: basal parts of left antlers, PIN 5126/100, 5126/101; incomplete distal tines, PIN 5126/102, 5126/103. Jaws with complete and incomplete cheek teeth rows: with P^2-M^3, PIN 5126/19, 5126/20, with P^2-M^2, PIN 5126/105; with P^4-M^3, PIN 5126/104; with D^2-D^4, PIN 5126/106; with P_2-M_3, PIN 5126/7, 5126/109, 5126/110, 5126/111, 5126/115; with P_4-M_2, PIN 5126/112; with M_2, PIN 5126/28. Limb bones: metacarpal, PIN 5126/113, distal part of metatarsal, PIN 5126/114.

Distribution: Late Miocene (Turolian, MN12), Russia.

Diagnosis: Differ from *P. asiaticus* in smaller size of the antler, a lower position of the first bifurcation, a larger angle of the first bifurcation, a stronger backward inclination of the beam, and a stronger forward inclination of the brow tine.

Description: The frontal in the holotype (PIN 5126/1; Table 1) is concave anterior to the pedicle. The pedicle is short, massive, slightly flattened in the transversal direction and lies almost in the plane of the forehead. The angle of the backward inclination is about 70°. The distance between the pedicles appears to be slightly greater than the horizontal diameter of the pedicle. The pedicles were weakly divergent. The angle of pedicle divergence is about 35–40°. The cross-section of the pedicle is rounded-triangular.

The holotype antler (PIN 5126/1; Fig. 2) is flattened, rather short, stout, and not widely divergent. The total antler span could be around 60 cm. The burr is large, tubercle-like, and oval in cross-section. The beam departs from the burr backwards and outwards. Its declination is of 55° towards the burr plane and of 10–12° to longitudinal axis of the pedicle. The angle of divergence at the base is more than 90°. The beam is curved upwards above the half of the distance between the first and second bifurcation. From the first bifurcation to the second, the anteroposterior diameter of the beam is gradually increasing. The outer surface of the beam is convex and the inner one is concave and flat. The beam bears a short ridge on its anterior edge, the cross-section being rounded-triangular in its base and

Table 1
Measurements (mm) of frontal and antlers of *Praesinomegaceros venustus* nov. sp.

Measurements		Holotype PIN 5126/1	PIN 5126/101	PIN 5126/100
Frontal	W	20	–	–
Pedicle	L	18.5	–	–
	DT	36.5	–	–
	DAP	39.7	–	–
Antler	L	+309.5	–	–
Burr	DT	54.4	53	50.7
	DAP	65.6	68.8	–
Antler base	DT	36	40	*ca.* 38
	DAP	62	62	+57.5
First bifurcation	H	45.8	52	–
First tine	L	+160	–	–
	DT	26.9	–	21
	DAP	44.1	–	30.5
Second tine	L	+175	–	–
	DT	22.8	–	–
	DAP	30	–	–
Second bifurcation	H	174.5	–	–

DAP: anteroposterior diameter; DT: transverse diameter; H: height; L: length; W: width.

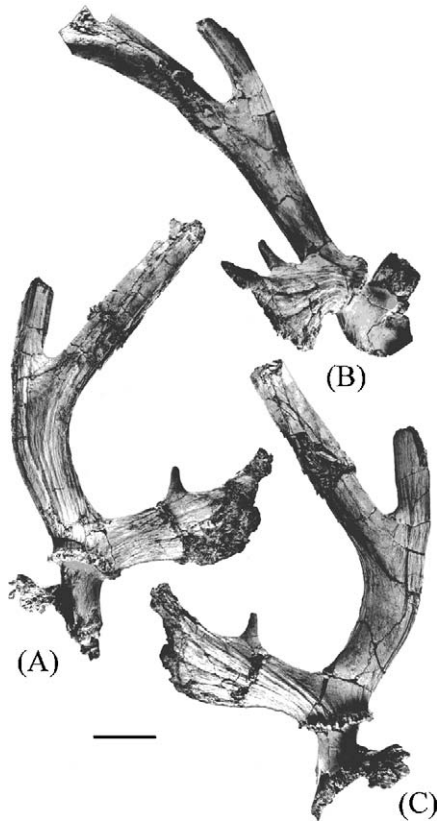

Fig. 2. Right frontal with antler, holotype of *Praesinomegaceros venustus* nov. sp. (PIN 5126/1) in (**A**) lateral, in (**B**) anterior, and (**C**) medial views. Scale bar = 5 cm.

flattened-oval at the bifurcation. The first bifurcation is very low. Its height is less than the anteroposterior diameter of the antler base. In *P. asiaticus*, the height of the first bifurcation is about 150% of the anteroposterior diameter of the antler base.

The brow tine is oriented anteroposteriorly and very weakly inclined medially. It is elongated, flattened and possesses a small accessory point at its upper (superior) border. From the anterior border of the beam, the brow tine runs forward and slightly outwards, and then curved upwards. The brow tine appears to have been relatively strongly turned upwards at its end. The brow tine is placed at an obtuse angle (105° in the holotype) to the beam (in *P. asiaticus* at an acute angle). The tine is enlarged to its broken end, the largest anteroposterior diameter placing ahead of its mid-length. The brow tine expansion is nearly vertical and set at angle of about 45° with the sagittal (median) plane of the skull. The cross-section of the brow tine base is flattened-oval, sharpened superiorly.

The distal portion of the beam is more flattened, enlarged anteroposteriorly and is divided into two flatten branches, directed outwards and forwards. These branches are rather long despite the missing ends.

The second bifurcation sets relatively low, slightly higher the mid-height of the antler. The angle of the bifurcation is about 40°.

A better preserved anterior branch (‘‘second’’ tine) is elongated and divides at its end into two tines, almost equal in size (judging from the sections of their bases). This anterior branch is more enlarged and more inclined forwards and outwards than the posterior branch. The length of the anterior branch before its dividing is larger than the distance between the first and second bifurcations. In its upper portion (the terminal fork), the branch is strongly turned outwards. The section of the anterior upper tine is pointed oval; the posterior upper tine section is oval.

The posterior branch (‘‘third’’ tine, or beam end) was apparently divided into two points: a stouter anterior one and a smaller and thinner posterior one. A longitudinal deep groove is present along the inner surface of the branch closer to its posterior edge. Both branches have a thickened anterior side and a narrow posterior edge. The cross-sections of their bases are rounded-triangular, with a shorter anterior side, a convex outer side and a concave inner side.

The surface of the antler is covered by sharp longitudinal grooves and ridges. They are less pronounced on the inner surface of the beam and upper branches. A distinct ridge along the posterior side of the beam begins at the level of its upward curvature and continues along the posterior edge of the posterior branch. A shorter ridge, beginning on the brow tine, disappears at the anterior side of the beam not very far from the first bifurcation.

The left antler base (PIN 5126/101) is broken above the first bifurcation and the tip of the brow tine is absent. The flattened brow tine branches off very close to the burr.

The right antler base (PIN 5126/100) is smaller, with the abrupt beam and brow tine in a short distance above the first bifurcation. The burr is irregular. The beam is rounded-triangular in section, with a wider and very weakly convex anterior side. The brow tine is distinctly enlarged anteriorly and inclined medially. The inclination is stronger than in the holotype. The antler possesses two accessory points in the space between the brow tine and beam base, the larger of them is placed at the outer edge of the bifurcation and the smaller (very rudimentary) one is in the middle of this space. The brow tine is flattened oval in section. The angle of the first bifurcation is 80°.

The incomplete anterior branch (PIN 5126/103) is divided into two abrupt tines. It is straighter than the anterior branch in the holotype, oval in cross-section with a thick anterior border.

The incomplete posterior branch (PIN 5126/102), broken close to the second bifurcation, is stouter than that in the holotype. It is strongly curved outwards. Its lateral surface is smoother than the medial one. The section of the base is rounded triangle, with a projecting anterior angle and a rounded posterior side. The upper portion probably was divided into a larger anterior tine and a smaller posterior tine.

The upper and lower cheek teeth rows are arched. The teeth are relatively low and weakly narrowed to the occlusal surface. The enamel is thick, rugose.

The upper premolars are enlarged labially, with a strong labial projection of the posterolabial angle of the crown (the postmetacrista occupies an oblique position; Fig. 3). The paracone and parastyle are strong. The metacone is less developed. The metastyle is thin. A distinct groove is present on the labial side of the premolars between the paracone and

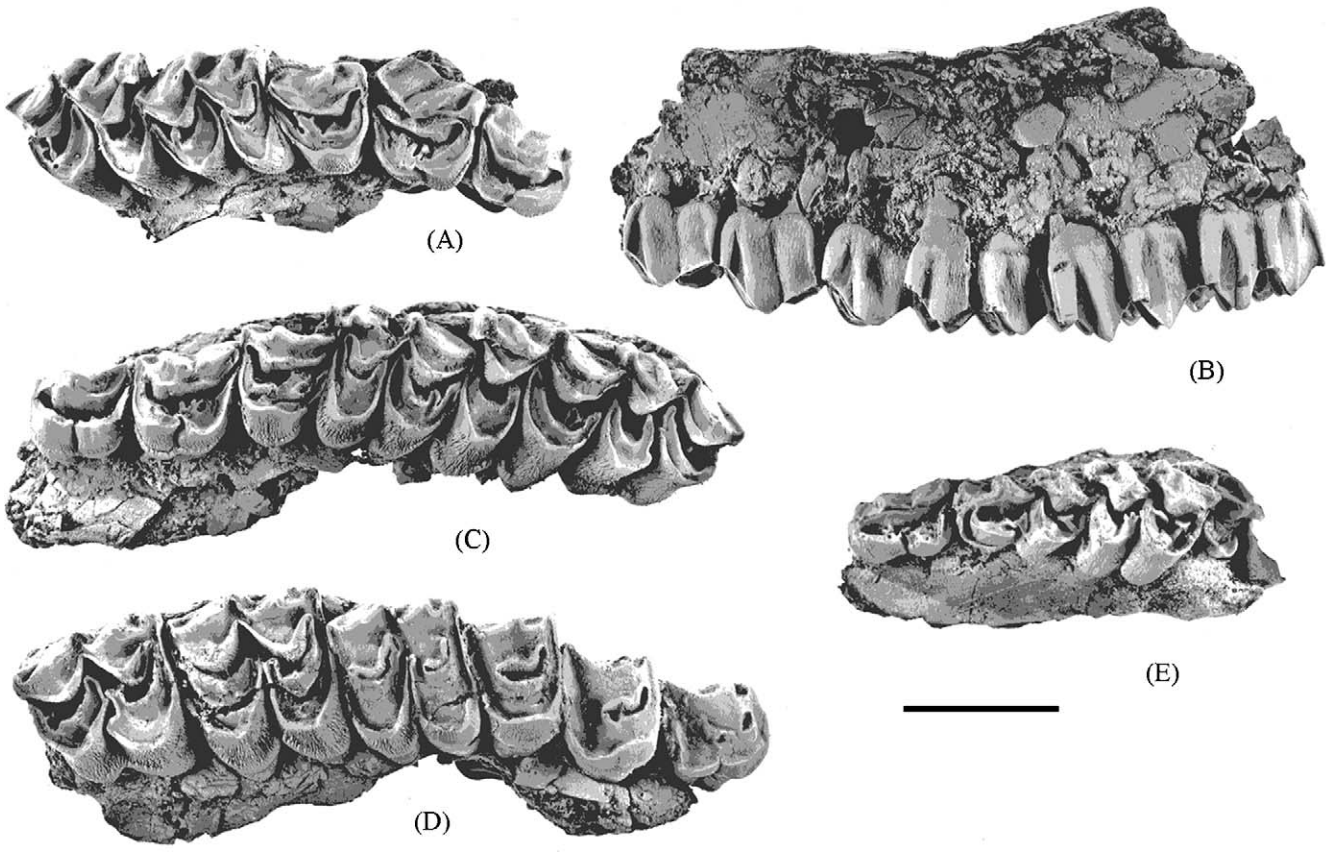

Fig. 3. Maxilla fragments of *Praesinomegaceros venustus* nov. sp.: (A) with P^2-M^2 (PIN 5126/105) in occlusal view; with P^2-M^3 (PIN 5126/19) in (B) labial and (C) occlusal view; (D) with P^2-M^3 (PIN 5126/20) in occlusal view; (E) with D2-D4 (PIN 5126/106) in occlusal view. Scale bar = 2 cm.

metacone. The labial pillars and grooves are slightly obliqued relative to the base of the crowns. On P^2 and P^3, the lingual crescents are split into two lobes. The bilobed pattern is better seen in unworn or weakly worn teeth, especially on P^2 and P^3. On P^4, only a scarcely visible furrow is present. The anterolingual cusp (protocone?) is well developed. On the unworn and weakly worn P^3 and P^4, the small folds (''wrinkles'') are present at the inner wall of an internal fossette.

The upper molars possess the well-developed parastyle, mesostyle, pillar of the paracone, and spur of the metaconule particularly strong on the slightly worn teeth. The pillar of the paracone and the mesostyle are enlarged to the base of the crowns where they are almost fused in some specimens (PIN 5126/20) forming a so-called horizontal basal bridge. According to Lister et al. (2005), this bridge is typical of megacerines. The fold of the protocone (postprotocrista *fide* Gentry et al., 1999; = protoconal fold *fide* Heintz, 1970) is weak, well distinct only on M^3. On M^1 and M^2, the posterior half of the crown is wider than the anterior half. M^2 is considerably larger than M^3. The crown of M^3 is narrowing posteriorly. The posterior side of the root of M^3 has the concavity and labial bridge similar to that in *M. giganteus* and *Dama* (see Lister et al., 2005). The entostyle is very low, not pillar-shaped.

The lingual cingulum in upper premolars and molars is well developed.

On upper milk teeth, all elements typical of permanent teeth are more pronounced. In addition to them, the mesostyle and the pillar of the metacone are very strong on D^3 and D^4.

The body of the mandible is low, with weak and moderate pachyostosis (Figs. 4 and 5). The index of the pachyostosis (depth/width ratio) is 138–162 below M_2, and 130–157.7 below M_3. The ventral border of mandible is strongly convex and the alveolar border is concave. The depth of the mandible slightly increased from P_4 to M_3. The foramen mentale is placed below P_2. The incisor part is narrow. The diastema between the lower canine and P_2 is fairly short.

P_2 is only a little smaller than P_3. Lower P_3 and P_4 show enlarged metaconid, without closing lingual valleys. The alae of the metaconid (praemetacristid and postmetacristid) are of approximately equal lengths. On P_3 and P_4, the fork of the paraconid (praeconulidcristid and postconulidcristid) is present. On P_2, it is not visible. All elements increase from P_2 to P_4. On lower premolars, the anterior and posterior labial cingulids are developed.

Lower molars lack the *Palaeomeryx* fold. The most developed element in their labial crescents is the metaconid; it is followed by a smaller entoconid, and then by the metastylid. The ectostylid is thin, pillar-like, and low; its height decreases from M_1 to M_3. The anterior cingulid is present.

The index of premolar length (premolar row/molar row ratio) in the upper jaw is about 74–78.6, in the low jaw 62–65. Measurements of the teeth are given in Tables 2–4.

Fig. 4. Mandible fragment of *Praesinomegaceros venustus* nov. sp.: with P_2-M_3 (PIN 5126/7) in A: occlusal; B: labial views. Scale bar = 2 cm.

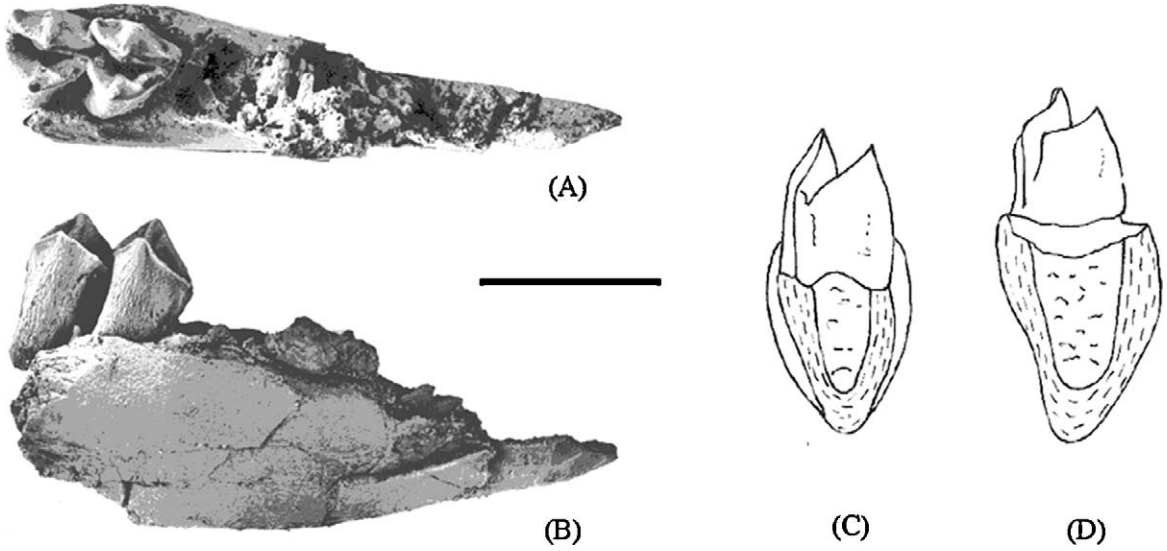

Fig. 5. Mandible fragments of *Praesinomegaceros venustus* nov. sp.: with M_2 (PIN 5126/28) in: A: occlusal; B: labial views; C: cross-section below M_2; D: with P_4-M_2, (PIN 5126/112) in cross-section below M_3. Scale bar = 2 cm.

The metapodials are relatively robust, with broad distal epiphyses (Fig. 6). The metacarpal (PIN 5126/113) is short. There are two oval facets (for metacarpals II and V) on the palmar surface at the proximal end of the bone. The distal epiphysis bears the sharp lateral and medial epicondyles. The distal trochlear crests are very strong on the palmar surface. The metacarpal measurements (in mm) are: length (L) = 186, transverse diameter of proximal epiphysis = 37.2, transverse diameter in the mid-length of the bone (DTm) = 28, transverse diameter of distal epiphysis (DTd) = 38.2.

Comparison: Differs from *P. asiaticus* in peculiarities of the antlers such as the obtuse angle and a very low position of the first bifurcation (its height is less than anteroposterior diameter of the antler base) and in smaller size.

Remark: It is unclear whether *P. asiaticus* and *P. venustus* nov. sp. belonged to the same phyletic lineage. The further study and additional fossil material could clarify this. The differences observed between both species correspond to the species level in extinct and extant genera of deer.

3. Discussion

3.1. Comments on megacerine phylogeny and evolution

The subfamily Cervinae comprises three tribes: the Pliocervini, Late Miocene-Pleistocene, Eurasia; the Megacerini, Late Miocene-Holocene, Eurasia; and the Cervini, Late Miocene-Recent, Eurasia (McKenna and Bell, 1997).

Table 2
Measurements (mm) of the upper teeth of *Praesinomegaceros venustus* nov. sp.

Measurements		PIN 5126/19	PIN 5126/20	PIN 5126/105	PIN 5126/104	Range	Mean	N
P^2-M^3		90	90.4	–	–	90–90.4	90.2	2
P^2-P^4		42.3	40	40.8	–	40–42.3	41.03	3
M^1-M^3		53.8	54	–	53.5	53.8–54	53.77	3
P^2	L	13.5	14	14	–	13.5–14	13.83	3
	W	12.2	13	13.6	–	12.2–13.6	12.93	3
P^3	L	13.8	13.4	15.8	–	13.4–15.8	14.3	3
	W	14.3	15.5	17.5	–	14.3–17.5	15.76	3
P^4	L	13.2	12	13.7	12.5	12–13.7	12.85	4
	W	14.9	16	15.7	16.3	14.9–16.3	15.7	4
M^1	L	19.2	17.5	17.8	16.7	16.7–19.2	17.8	4
	W	18.3	19.2	18.5	19	18.3–19.2	18.75	4
	WAL	8	8.4	7.6	7.5	7.5–8.4	7.88	4
	WPL	10	9	9.5	8.6	8.6–10	9.27	4
M^2	L	20	19.5	19.5	20.5	19.5–20.5	19.88	4
	W	22.5	22.5	21.6	23	21.6–22.5	22.4	4
	WAL	8.5	9.6	8	10.4	8–10.4	9.01	4
	WPL	11.4	11.2	10.7	11.8	10.7–11.8	11.27	4
M^3	L	19	19.5	–	19.5	19–19.5	19.3	3
	W	21	20.7	–	20	20–21	20.57	3

Abbreviations as in Table 1 plus N: sample size; WAL: width of anterolingual lobe of molar; WPL: width of posterolingual lobe of the molar.

Table 3
Measurements (mm) of the upper milk teeth of *Praesinomegaceros venustus* nov. sp. Abbreviations as in Table 1.

Measurements	D^2-D^4	D^2		D^3		D^4	
	L	L	W	L	W	L	W
PIN 5126/106	43.7	14.4	10	17	11.5	16.5	15.6

According to less popular alternative classification based on extant species, the Cervinae is composed of two tribes, the Muntiacini and Cervini (Cap et al., 2002; Gilbert et al., 2006). The last taxon of this classification corresponds only to a part of the Cervini *fide* McKenna and Bell (1997) and this paper, and does not include a bulk of fossil genera. According to paleontological data, the closely related muntiacines and cervines undoubtedly belong to two different subfamilies, Muntiacinae and Cervinae (Viret, 1961; Vislobokova, 1990; McKenna and Bell, 1997). The relationships of *M. giganteus* with extant Cervini is hotly debated (e.g., Lister et al., 2005; Kuehn et al., 2005).

Megacerines are characterized by a number of peculiar features which well distinguish them from the other Cervinae. But judging from the type of the vomer in the skull, a plesiometacarpal foot structure, and DNA evidences, they undoubtedly belong to that subfamily.

The systematics of megacerines is based mainly on the antler morphology. Antlers are used by males in combats and for displays and underwent considerable changes in the evolution of the deer. The main trends of antler evolutionary development are related to their increase, tissue growth, biomechanics, and ecology as well as the necessity in more performance (imposing

Table 4
Measurements (mm) of the lower teeth of *Praesinomegaceros venustus* nov. sp. Abbreviations as in Table 2.

Measurements		PIN 5126/7	PIN 5126/112	PIN 5126/109	PIN 5126/110	PIN 5126/111	PIN 5126/115	Range	Mean	N
P_2–M_3		103.2	–	99.2	97	95	102.2	95–103.2	99.3	5
P_2–P_4		40.2	–	36.8	40.2	38.5	40.2	36.8–40.2	39.2	5
M_1–M_3		64.8	–	61.7	61.7	61.1	64.8	61.1–64.8	62.8	5
P_2	L	13.5	–	12	11.6	11.8	12.1	11.6–13.5	12.2	5
	W	7.4	–	6.8	6.8	6	7	6–7.4	6.8	5
P_3	L	15	–	14	14.8	14.6	14.2	14–15	14.5	5
	W	8.5	–	9.4	7.7	9.3	8.8	7.7–9.4	8.7	5
P_4	L	15.2	15	14.5	16.2	13.3	16	13.3–16.2	15.03	6
	W	8.4	8.6	10.4	9.3	10.5	10.6	8.4–10.6	9.63	6
M_1	L	17.2	18.2	17.2	18	18.2	17.4	17.2–18.2	17.7	6
	W	11.6	11.7	11.6	11	11.7	12.6	11–11.7	11.7	6
M_2	L	19.2	20	19.8	19	18.8	19.2	18.8–20	19.3	6
	W	12.8	13.5	12.5	13	12.6	14	12.5–14	13.06	6
M_3	L	27.4	–	27	25.4	23.7	26.2	23.7–27.4	25.94	5
	W	13.2	–	14.5	12.9	12	13	12–14.5	13.12	5

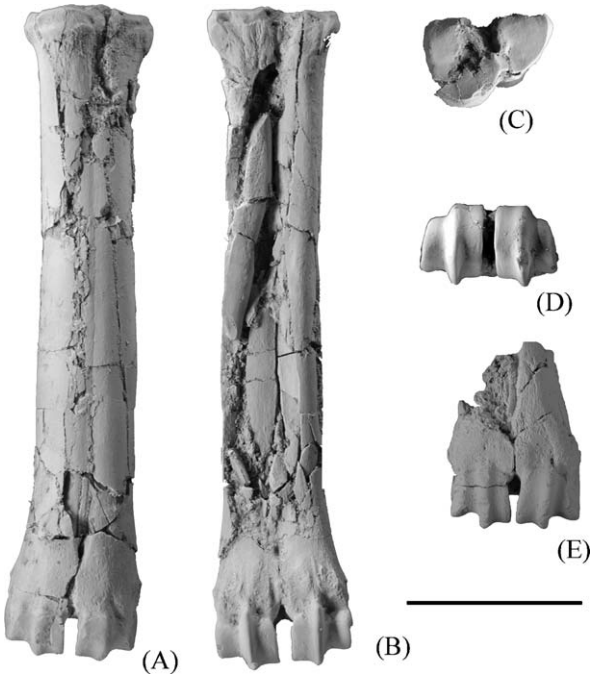

Fig. 6. Limb bones of *Praesinomegaceros venustus* nov. sp.: metacarpal (PIN 5126/113) in A: anterior; B: palmar; C: proximal; D: distal views; E: partial metatarsal (PIN 5126/114) in anterior view. Scale bar = 5 cm.

view). In most megacerine genera, the distal part of the antlers expands into a palmation, very impressive in *M. giganteus* (Blumenbach, 1803), *Sinomegaceros pachyosteus* (Young, 1932), and *S. flabellatus* (Teilhard de Chardin, 1936) (Zdansky, 1925, 1928; Young, 1932; Teilhard de Chardin, 1936; Teilhard de Chardin and Pei, 1941; Gould, 1973; Geist, 1999; Lister, 1994; Van der Made, 2006). Similar to other cervines, megacerines demonstrated high individual variability in antler structure. Nevertheless, the basic branching pattern of the antlers in different genera was rather constant.

Despite a variety of contradictive views on megacerine history, almost all students recognize the existence of two groups in the Pleistocene of Europe: a first one connected with *M. giganteus*, and a second one with *M. verticornis* (Dawkins, 1872; Azzaroli, 1953, 1979; Radulesco and Samson, 1967; Vislobokova, 1981; Azzaroli and Mazza, 1992; Abbazzi, 2004). To the group of *M. giganteus*, Azzaroli (1953) attributed *M. antecedens* (Berckhemer, 1941) and *M. savini* (Dawkins, 1887) (= *Praedama savini*) from Europe and four Asiatic species (*M. pachyosteus*, *M. flabellatus*, *M. ordosianus* Young, 1932, and *M. yabei* (Shikama, 1938), all included here in *Sinomegaceros*). Apart from *Praedama* and *Sinomegaceros*, a closely related genus to the group is *Arvernoceros* (Heintz, 1970; Vislobokova, 1981; Vislobokova and Hu, 1990).

The megacerine phylogeny, when it is based only on European species, is very incomplete. It was supposed that the group of *M. giganteus* was of uncertain origin and the group of *M. verticornis* (here *Praemegaceros verticornis* group) was derived from *Eucladoceros* (Azzaroli and Mazza, 1992; Abbazzi, 2004). The parsimony cladistic analysis showed a monophyly (close relationship) of *M. giganteus* and *M. verticornis* and their distance from other cervines (Pfeiffer, 2002; but see Lister et al., 2005 for a different opinion).

All members of the group of *M. giganteus* possess divergent pedicles, which generally set near one another, hollowed frontals in front of the pedicles, and a flattened brow tine branching off closely near the burr (Azzaroli, 1953).

The *Praemegaceros verticornis* group is characterized by divergent pedicles which set wide apart and directed obliquely backwards, a flat or convex forehead, and a subcylindrical brow tine at some distance from the burr and strongly bent forwards (Azzaroli, 1953).

A phylogenetic model of megacerines beginning from 1.2 Ma was presented recently by Van der Made and Tong (2008). According to their study, *Megaloceros* and *Sinomegaceros* are separate genera and differ distinctly in origin and morphology of the antler distal (terminal) palmation: in *Megaloceros*, the distal palmation is formed from a bifurcated third tine, while in *Sinomegaceros*, the palmation represents a distal continuation of the main beam.

As in other cervines, the increase of size and elongation of megacerines antlers led to its larger backward or outward inclination and larger divergence, a wider angle of the first bifurcation, and the changes in brow tine size, position, orientation, etc. In megacerines, the brow tine and terminal palmations developed on the background of these changes. The changes in antler structure were accompanied by the shortening and thickening of the pedicles and changes in their position and direction.

The main trends in the evolutionary development of the antlers depend on many factors including those of biomechanics and ecology. In some lineages of the Cervini, a gradual lowering of the first bifurcation is traced (e.g., *Cervus pardinensis-C. philisi-C. perolensis*: Heintz, 1970). The variability in the first bifurcation height in *Praesinomegaceros* inherited from *Cervavitus* appears to have been very important for further biodiversity of the Megacerini. Along with other characters, this feature has provided the appearance of several lineages within the group.

Praesinomegaceros displays the most primitive pattern of antler structure yet known in megacerines. The most important features of that pattern are the following: the weak backward inclination and relatively weak divergence of the antler, and an anterior bend of antler upper portion. *Praesinomegaceros* also is primitive in the shape and lower position of the brow tine (its anteroposterior orientation, medial inclination, elongation, and relatively large size), low position and narrowness of the second bifurcation, and probably in the absence of the terminal palm. In deer, the terminal palmation clearly increased with ages. Judging from the data on the ontogeny of deer with palmated antlers (*Cervavitus*: Alexejev, 1915; Korotkevitsch, 1970; *Sinomegaceros*: Shikama and Tsugawa, 1962), it is not excluded that a weak narrow palm might be present in some older individuals of *Praesinomegaceros*.

Praesinomegaceros with its divergent pedicles, concave forehead, and low-placed and palmate brow tine of the antlers, falls into the group of *M. giganteus* (Vislobokova, 1990; Vislobokova and Hu, 1990).

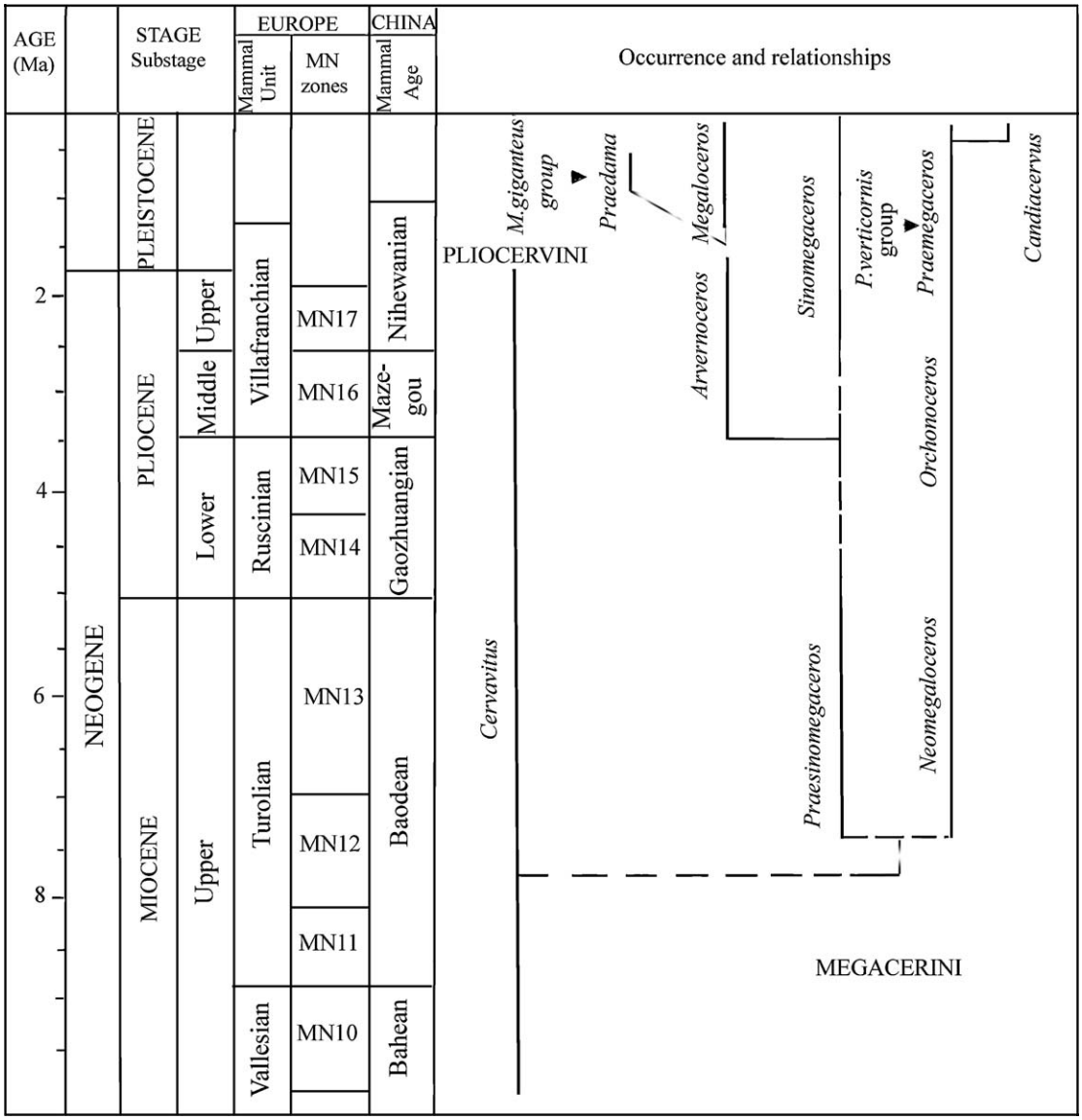

Fig. 7. Occurrences and relationships of the Megacerini.

Of all known members of the *M. giganteus* group, the closest in morphology to *Praesinomegaceros* is *Sinomegaceros* (Fig. 7). It was similar to *Praesinomegaceros* in many important characters including a rather short muzzle, an anterior bend of the beam, a medial inclination of the brow tine base, enlarged molars, and mandible and teeth structure.

The narrowness of the second bifurcation in *Praesinomegaceros* approaches that of the terminal palm in the most ancient and primitive *Sinomegaceros* – *S. tadzhikistanis* Vislobokova, 1988 from the Late Pliocene of Kuruksai (MN17, 2.2–2.0 Ma), Tadjikistan, and *S. konwanlinensis* Chow, Hu and Lee, 1965 from the Early Pleistocene of Gongwangling (*ca*. 1.3 Ma), Shaanxi (Hu and Qi, 1978; Vislobokova, 1988). The weak anteroposterior expansion of the brow tine in *Praesinomegaceros* is close to that in *S. tadzhikistanis*. The antler structure in *Sinomegaceros* may be regarded as an evolutionary sequel of that in *Praesinomegaceros*. Apart from the increase in size, the antler transformation from *Praesinomegaceros* to *Sinomegaceros* could be performed through:

- outward bend (turnings) of the upper portion of the antler and the brow tine;
- elongation of the beam (it remains short in some *S. flabellatus*);
- fusion of the anterior and posterior branches of the upper portion of the antlers into the palm and its further enlargement, with the greatest palmate crown in *S. pachyosteus*;
- gradual change of the position of a brow tine base from vertical (along the anterior border of the beam) to inclined medially (*S. tadzhikistanis*, *S. konwanlinensis*), and then to transverse (adult *S. pachyosteus*, *S. flabellatus*);
- anteroposterior brow tine widening accompanied by its twisting outside and up to take a position perpendicular to the sagittal plane of the head (*S. pachyosteus*, *S. flabellatus*).

Apart from close relationships with *Sinomegaceros,* the structure of the antlers of *Praesinomegaceros* provides evidence on the evolution of other megacerines too. Within the group of *M. giganteus,* two main evolutionary trends based on the primitive pattern typical of *Praesinomegaceros* are recognized. They are represented by two different character sets (combinations):

- A lower antler portion is mainly inclined posteriorly (backwards); the terminal palm remains relatively narrow; the brow tine in advanced forms becomes strongly enlarged; the anterior medial tine (''second'' tine) and back tine are usually absent (representatives: *Arvernoceros*, *Sinomegaceros*; first occurrence: Late Pliocene, *ca*. 3 Ma). *Arvernoceros* and *Sinomegaceros* differ in the brow tine shape and teeth structure. In *Arvernoceros*, the brow tine is not strongly enlarged and oriented anteroposteriorly as in *Praesinomegaceros*, while in *Sinomegaceros*, it resembles that in *Praesinomegaceros* only in the early forms (*S. tadzhikistanis* and *S. konwanlinensis*) and becomes very large, transversely and vertically oriented in the later species (*S. pachyosteus*). In *Arvernoceros* and *S. konwanlinensis*, the brow tine bears an additional tine (Heintz, 1970; Hu and Qi, 1978). This character is similar to that in *Praesinomegaceros*;
- the antler is more inclined laterally (outwards); the terminal part (palm) is considerably enlarged, whereas the brow tine remains relatively narrow and in some advanced forms even decreases in size; the anterior medial tine (''second'' tine) and back tine are usually present (representatives: *M. giganteus*, *Praedama savini*; first occurrence: 1.2 Ma). In *M. giganteus*, the brow tine often retains the bifurcation. A large expansion of the brow tine in the species is very rarely traced. This is known only in the earliest specimens from the Holsteinian of Steinheim (Germany; *ca*. 400 or 300 kyr BP; Berckhemer, 1941; Lister, 1994: Fig. 18E).

The early representatives of both evolutionary trends as well as some young individuals of even advanced species show more similarities with the primitive state found in *Praesinomegaceros*. All early representatives of both trends had a medial inclination of a brow tine base as in *Praesinomegaceros*. This state is traced in *Arvernoceros, S. konwanlinensis*, and *Praedama savini*. The medial inclination of antler base is also seen in the very young individuals of *M. giganteus* (Van der Made and Tong, 2008). In older (fully adult) *M. giganteus*, a brow tine palmation dips laterally or its base occupies a transversal position due to a larger antler divergence.

The appearance of the anterior medial tine is more typical of the second evolutionary trends. It is present in the antlers of adult *Megaloceros* and *Praedama*. The posterior (back) tine in the first branches appears to have been present only in *S. yabei.* The antler complication through the appearance of additional tines in advanced megacerines obviously resembles that in recent cervines (an example of homoplasy).

There is a definite resemblance between *Praesinomegaceros* and earliest *Praedama, P.* aff. *savini* from Libakos (Van der Made and Tong, 2008: Fig. 7, 3a, b). The antler of this type could be originated from an antler typical of *Praesinomegaceros* through a stronger inclination of its anterior terminal branch forwards and its posterior terminal branch (beam end) backwards. The further stage of development of these antlers might be the formation of the palmation through the fusion of both branches and its enlargement. This corresponds to the development of the terminal palm in *M. giganteus*. It seems quite plausible that the back tine in the antlers of *M. giganteus* could be developed from a small posterior tine of the posterior branch of the antlers of *P. venustus* nov. sp.

3.2. *Praesinomegaceros* and *Cervavitus*

The roots of Asiatic megacerines go back into the Pliocervini, comprising most primitive members of the subfamily Cervinae. This group, intermediate in its characters between the Muntiacinae and Cervinae, was introduced by Khomenko (1913) at the subfamily level but is now regarded as a separate tribe within the Cervinae (Vislobokova, 1990; McKenna and Bell, 1997; Petronio et al., 2007). Along with characters typical of the Miocene muntiacines (long pedicles in the forehead plane, long upper canines in males, brachyodont teeth, and *Palaeomeryx* fold in lower molars), pliocervines share with other cervines important apomorphies: elongated antlers with not less than three points and a well-developed beam.

Praesinomegaceros bears a strong antler and dental resemblance with the pliocervine *Cervavitus* Khomenko, 1913, which occurred in central Eurasia in the Late Miocene-middle Pliocene (MN10-16) and survived in China up to the Early Pleistocene. But being similar in size with the living fallow deer *Dama dama* (Linnaeus, 1758), *Praesinomegaceros* is distinctly larger than *Cervavitus. Praesinomegaceros* inherited many characters typical of *Cervavitus*: antler flattening, long flat first tine, presence of small basal accessory points, shallow mandible, arched cheek tooth rows, etc. But these characters are combined with megacerine features traced in morphology of its skull, antler, teeth, and limbs. As compared with *Cervavitus*, *Praesinomegaceros* is more advanced in the absence of supraorbital ridges, more massive and less backward inclined pedicles, the direction of the upper branches upwards and forwards (in *Cervavitus* backwards), a larger angle of the first bifurcation, relatively shorter lower premolar and longer upper premolar rows, considerably enlarged M^2, the absence of the *Palaeomeryx* fold, more hypsodont cheek teeth, less inclined and broader lingual crescents in upper molars, and labial crescents in lower molars. Typical of megacerines the horizontal basal bridge in upper molars (Lister et al., 2005), seen in some specimens of *Praesinomegaceros*, is reminiscent of that in *Cervavitus* but in the higher crowns condition.

Which of known *Cervavitus* species could be a direct ancestor of *Praesinomegaceros* today is unclear.

Praesinomegaceros venustus is very similar to *Cervavitus variabilis* (Alexejev, 1913) from the Late Miocene of Novoelizavetovka (MN12), Ukraine, in the shape and position of the brow tine but differs from it by many other features including the further bifurcation of the second and third tines (beam point), an anterior and lateral twisting of the antler upper

portion, and on the whole more advanced morphology of cheek teeth, but combined with a primitive P_4 (with a short, not enlarged metaconid).

In the structure of cheek teeth, *P. venustus* nov. sp. resembles *Cervavitus novorossiae shanxius* Dong and Hu, 1994 (= *C. shanxius*; Petronio et al., 2007) from the Late Miocene of the Hounao locality (Mahui Formation, 6–5.4 Ma; Flynn et al., 1991), Yushe, Shanxi. They are similar in size and proportions of upper premolars, the presence of two lingual lobes on P^2 and P^3, and even in the absence of the *Palaeomeryx* fold (in most *C. shanxius*), but well distinguished in size and structure of molars. In addition, *C. shanxius* differs from *Praesinomegaceros* by smaller body size and higher position of the first and second bifurcations of the antlers.

A number of similar features in teeth structure of *P. venustus* nov. sp. and *C. shanxius* could be obtained in parallel due to the same evolutionary trends in similar environments. In the level of decrease of the fold of the protocone and reduction of the cingulum, *C. shanxius* surpassed not only other species of the genus but *Praesinomegaceros* too. The ancestor of *Praesinomegaceros* appears to have been among more primitive species of *Cervavitus* with a weak molarized P_4, probably close to a weakly specialized *C. novorossiae* Khomenko, 1913 from the Late Miocene of Taraklia (MN12), Moldova.

3.3. Cervavitus-Praesinomegaceros *transition - Main apomorphies*

The transition from *Cervavitus* to *Praesinomegaceros* was accompanied by a number of essential changes in skull, antler, dentition, and limb bones, which determined the main trends of the megacerine evolution. The most important apomorphies are the following:

- **elongation and anterior bend of the beam in the antlers**. This feature well separates *Praesinomegaceros* from *Cervavitus.* As in *Praesinomegaceros*, an upper portion of the antlers is curved anteriorly in *Sinomegaceros* and *Arvernoceros.* Although in fully adult *M. giganteus*, the palmation curves outwards and downwards due to a great divergence and twisting of the antlers, in some young *M. giganteus*, it still directed anteriorly (Van der Made and Tong, 2008);
- **pachyostosis in mandible**. In *Praesinomegaceros*, the index of mandible pachyostosis corresponds to its value in other megacerines and quite differs from those in *Dama*, *Capreolus*, and *Cervus* (Van der Made and Tong, 2008: Fig. 14) as well as in *Cervavitus*. The index of pachyostosis below M_3 in *Praesinomegaceros* (130–157.7) coincides with that in *M. giganteus* and is at the upper part of its range in *S. pachyosteus* (see Van der Made and Tong, 2008: Fig. 14, the depth is measured lingually).

The pachyostosis in *Praesinomegaceros* could be stimulated, on the one hand, by the increase of molars in a shallow dentary and, on the other hand, by an increasing vertical load in the skull and mandible, owing to a larger antler weight (especially that of the lower part of the antlers). An extreme increase of that part of the antlers in Pleistocene *S. pachyosteus* from the Middle Pleistocene of Zhoukoudian (Choukoutien, Loc. 1, 0.7–0.3 Ma) is well correlated to an extreme pachyostosis of its skull and mandible. In some individuals of this species, the body of the mandible below M_3 becomes more or less circular in transverse section, the index range is 109.8–155.9 (Young, 1932, the depth could be measured buccally).

In megacerines, the pachyostosis first developed through the mandible body widening and then through the increase of the bone density. The last step is revealed in *M. giganteus* and *S. pachyosteus* ontogeneses. The juvenile forms of *M. giganteus* have not highly pachygnathous mandibles but they can be much more pachygnathous in older individuals (Lister, 1994; Pfeiffer, 2002). In *S. pachyosteus,* the mandible pachyostosis also increases with age (Young, 1932). *Sinomegaceros* considerably surpassed *Megaloceros* in pachyostosis. The presence of pachyostosis in young individuals of *Praesinomegaceros* supports its closer relationship with *Sinomegaceros*;

- changes in cheek teeth structure. Many changes in cheek teeth in the *Cervavitus-Praesinomegaceros* lineage correspond to their main evolutionary differences with other cervines: increase in size, increase in hypsodonty, increase of the occlusal surface, decrease of premolar/molar rows ratio, disappearance of the *Palaeomeryx* fold, decrease of the protoconal fold, etc. In all these characters, *Praesinomegaceros* is more advanced than *Cervavitus*. In addition, *Praesinomegaceros* is well differentiated from *Cervavitus* in having more developed biloby of the upper premolars, relative larger molars, decrease of the entostyle in upper molars, thinning and decrease of the ectostylid in lower molars, and enlargement of labial crescents in upper molars and lingual ones in lower molars (they became less sharpen than in *Cervavitus*). All these characters together with low mandible body and weakly molarized P_4 were inherited by *Sinomegaceros*:
  - the increase of bilobed pattern in upper premolars. A well developed biloby on P^2 and P^3 in *Praesinomegaceros* reflects a greater level of their molarization (enlargement of the metaconule) as compared with that in *Cervavitus*. This provides the increase of the occlusal (masticatory) surface. The biloby on P^2 and P^3 is also well expressed in *S. konwanlinensis*, *Arvernoceros*, and *Orchonoceros*; it is variable in *S. pachyosteus* and decreases in *M. giganteus* (Young, 1932; Heintz, 1970; Hu and Qi, 1978; Vislobokova, 1983),
  - a considerable anteroposterior enlargement of the posterior halves of the crowns of upper molars. The increase of the upper molars in *Praesinomegaceros* was generated by a considerable enlargement of the posterior halves of the crowns: they become wider than the anterior halves. The character is well pronounced in *Sinomegaceros* as well as in other megacerines (*Arvernoceros, Orchonoceros*). This is well seen in *M. giganteus*. In *Cervavitus*, the anterior and posterior halves of the crowns usually are approximately equal in width. The tendency to the widening of the crown

posterior half is traced in some *Cervavitus* from Loc. 35, Yushe (Zdansky, 1925: Pl. 7, Fig. 1),
  - an outstripping increase of M^2 in comparison with M^3. In early megacerines (*Arvernoceros ardei*, *Sinomegaceros pachyosteus*, *Praedama savini*), M^3 remains smaller than M^2, as in *Praesinomegaceros*. The small size of M^3 in *P. savini* appears to be the primitive state, but not the result of reduction. In other megacerines, M^2 and M^3 become again almost equal in size (as in *Cervavitus*) although M^3 usually remains smaller than M^2;
- **robust metacarpals**. A quite distinct character of megacerine metapodials is the broad form of the distal epiphysis (Azzaroli, 1953). The character is well expressed in *Praesinomegaceros* as well as a considerable massiveness of the bone in the mid-length. The metacarpals in *Praesinomegaceros* are longer and more robust than that in *Cervavitus*. Being approximately equal in length to that in *Dama dama*, *Praesinomegaceros* metacarpal is much wider (see Pfeiffer, 1999: Abb. 100). *Praesinomegaceros* massiveness of the bone approaches *Sinomegaceros* and other megacerines one. The robusticity index (DTd/L) of *P. venustus* nov. sp. metacarpal (20.54) is above those of *Cervavitus variabilis* (15.7–16.6), *Dama* and *Cervus*, and corresponds to its values in some other megacerines (with L = 5DTd; Van der Made and Tong, 2008: Fig. 22). The index of massiveness of the bone in its mid-length in *Prasinomegaceros* (DTm/L = 15.05) surpasses that in *Cervavitus* (9.7–9.8);
- **a plesiometacarpal type of reduction of metacarpals II and V**. *Cervavitus* has the vestigial lateral metacarpals along or almost along the whole length of the canon bone (Alexejev, 1915; Zdansky, 1925; Dong and Hu, 1994). *Praesinomegaceros* shares a plesiometacarpal foot structure with megacerines, most of recent cervines (Cervini), and some advanced Muntiacinae (Muntiacini). The plesiometacarpal state apparently arose within these groups in the Late Miocene as the result of parallel evolution. The plesiometacarpal state in the Megacerini and Cervini is based on the holometacarpal condition in their pliocervine ancestors.

3.4. Ecology

Similar to *Cervavitus* (Korotkevitsch, 1970; Petronio et al., 2007), the earliest megacerines were apparently associated with ecotonal environments (between woody and more open areas). *Praesinomegaceros*, with its relatively (fairly) narrow antlers, dental and postcranial characters, might be well adapted to the woodland habitats.

Praesinomegaceros, like *Cervavitus*, was a browser. Browser adaptations are well seen in its short muzzle, short diastema, arched cheek teeth, shallow mandible, low level of P_4 molarization, molar basal pillar reduction, rather thick enamel, and well developed cingulum. However, the absence of the *Palaeomeryx* fold in lower molars and the fold of the protocone in upper molars in *Praesinomegaceros*, contrasting with *Cervavitus*, indicates its feeding on coarser food and plausibly an initial shift to mix-feeding. Possessing molarized upper premolars and enlarged molars, *Praesinomegaceros* was able to chew a larger volume of plant food in comparison with *Cervavitus*. A diet of *Cervavitus* appears to have consisted from soft juicy leaves of trees and shrubs with additions of fruits and seeds (Korotkevitsch, 1988). In addition, *Praesinomegaceros* could feed on wood and shrub bark and branches as well as on some herbs and possibly grass.

In the course of their evolution, megacerines gradually acquired some grazer (mix-feeder) adaptations: premolar row became shorter, posterior molars enlarged, hypsodonty increased, enamel became denser and thinner, etc. The development of these adaptations was parallel in various evolutionary lineages, with different rates. The most adapted species towards grazing were *M. giganteus* and *S. yabei* (Van der Made and Tong, 2008). *Praedama savini* in feeding adaptations probably remained most close to *Praesinomegaceros*; it resembles *Praesinomegaceros* in relatively thick enamel, large premolars, weakly molarized P_4, and small posterior molars. Van der Made and Tong (2008) supposed that *P. savini* was adapted to a coarse and hard food ''that needs to be masticated with great pressures''.

Cervavitus probably was a saltatorial runner. In proportion and relative sizes of limb bones, it was close to the fallow deer *Dama dama* (Linnaeus, 1758), and sika deer *Cervus nippon* Temmnick, 1837 (Korotkevitsch, 1988). The increase of the relative massiveness of metapodials and enlargement of their distal ends in *Praesinomegaceros* in comparison with those in *Cervavitus* could be related with the increase of the body weight and the greater loads in the distal segments of limbs. These features may indicate a faster locomotion on rather wet grounds and in more open landscapes and may represent a first step towards cursorial running presumed in *M. giganteus*. This mode of running is typical of extant deer living in open spaces. There is a definite resemblance between *Sinomegaceros* and *Rangifer* in the broadened distal parts of metapodials. Based on this, Young (1932) even supposed that *Sinomegaceros* could be ''a swamp animal''.

3.5. Megacerine origin

According to some authors, the first appearance of unquestionable megacerines was in the middle part of the Early Pleistocene (about 1.4 Ma) and that of *M. giganteus* and related oriental forms in the late Middle Pleistocene (about 0.4 Ma; Abbazzi, 2004; Lister et al., 2005). This is quite right when looking at European species. However, paleontological evidence from central Eurasia shows that the first appearance of megacerines occurred much earlier. New data on *Praesinomegaceros* confirm the Late Miocene origin of the group. These data relative to Megacerini and paleontological evidence concerning Cervini testify the Late Miocene time of origin of both groups.

Of the known representatives of the Pliocervini, the most suitable ancestor of megacerines is *Cervavitus*. Now it is evident that this deer gave origin not only to the tribe Megacerini but also to many fossil and recent cervine genera within the tribe Cervini. First introduced by Flerov (1952), this hypothesis was confirmed by Vislobokova (1990) and has

found supports in recent investigations. For instance, the living *Axis* and *Rusa* are recognized to be allied with the Chinese pliocervines (Petronio et al., 2007).

The origin of the Megacerini and Cervini is connected with the adaptive radiation of *Cervavitus*. A great variability of *Cervavitus* antler and dental morphology was the base for the appearance of a number of new trends in the evolution of cervines. The change in environments, considerable enlargement and differentiation of the biotopes, cooler climate at the end of the Miocene led to the evolutionary shift within *Cervavitus* which gave origin to a number of more advanced forms including the first megacerines.

3.6. Megacerini and their close living relatives

Looking at the closest relatives of megacerines among extant deer, a number of phylogenetic analyses based on DNA evidence and morphological data gave controversial results. According to one group of researchers, *M. giganteus* had a sister-group relationship with the living fallow deer, *Dama dama* (Lister et al., 2005; Hughes et al., 2006), while others showed it was closer to the red deer or wapiti, *Cervus elaphus L.* (Kuehn et al., 2005). The parsimony analysis based on cranial, antler, dental, and postcranial data revealed a closer relationship of *M. giganteus* with *Cervus* and its deep divergence with *Dama* (Pfeiffer, 2002).

Calibrated divergence times on the basis of molecular data also differ and need correction in accordance with paleontological evidence. According to Pitra et al. (2004), the deep divergence in mtDNA indicates that the *Dama-Megaloceros* split could be placed at about 4-5 Ma (assuming a divergence of the muntiacine and cervine deer at about 7 Ma; Pitra et al., 2004). However, the event was obviously much older (probably mid-Turolian) because the first cervine (*Cervavitus*) appeared at the very beginning of the Late Miocene (Vallesium, MN 10, about 10 Ma). Li et al. (2003) refer the divergence time of mtDNA haplotypes among the subfamilies in the Cervidae and within the subfamily Cervinae to date 6–10 and 2–7 Ma, respectively.

Within the recent cervines, there is a great scope for parallel evolution from a primitive cervine group. The similarities at the morphological and molecular levels between *M. giganteus* and some living cervine deer (*Dama* and *Cervus*) could be achieved due to common ancestor archetype and parallel evolution (or be result of homoplasy: Pfeiffer, 2002). *Cervus* and *Dama* are really the closest living relatives of *M. giganteus*. However, they are removed from it in the long ways (traits) of separate evolution, beginning with the divergence of the Pliocervini into the Megacerini and Cervini in the Late Miocene. The common *D. dama*, in my opinion, is not a primitive megacerine. Apart from many antler and skull characters non-typical of megacerines, it lacks one of the main megacerine characters – the pachyostosis in the mandible.

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References

Abbazzi, L., 2004. Remarks on the validity of the generic name *Praemegaceros* Portis, 1920, and an overview on *Praemegaceros* species in Italy. Atti della Academia nazionale dei Lincei, Rendiconti Lincei, Classe di Scienze Fisiche. Matematiche e Naturali 15, 115–132.

Alexejev, A.K., 1913. About a new form of deer from the neighborhood of village Petroverovka. Zapiski Novorossijskogo Obschestva estestvoispytatelej 40, 1–13 [in Russian].

Alexejev, A.K., 1915. Fauna of the vertebrates of the v. Novo-Elizavetovka, Tekhnik, Odessa, [in Russian].

Azzaroli, A., 1953. The deer of the Weybourn Crag and Forest Bed of Norfolk. The Bulletin of the British Museum (Natural History) 2, 3–96.

Azzaroli, A., 1979. Critical remarks on some giant deer (genus *Megaceros* Owen) from the Pleistocene of Europe. Palaeontographica Italica 71, 5–16.

Azzaroli, A., 1994. Forest Bed elks and giant deer revisited. Zoological Journal of the Linnean Society 112, 119–133.

Azzaroli, A., Mazza, P., 1992. On the possible origin of the giant deer genus *Megaceroides*. Atti della Academia nazionale dei Lincei, Rendiconti Lincei, Classe di Scienze Fisiche. Matematiche e Naturali 3, 23–32.

Berckhemer, F., 1941. Über die Riesenhirschfunde von Steinheim an der Murr. Jahresheft des Vereins für vaterländische Naturkunde in Württemberg 96, 63–88.

Cap, H., Aulagnier, S., Deleporte, P., 2002. The phylogeny and behavior of Cervidae (Ruminantia, Pecora). Ethology Ecology Evolution 14, 199–216.

Dietrich, W.O., 1933. Review of Young, C.C.: On the Artiodactyla from *Sinanthropus* site at Choukoutien. Neues Jahrbuch für Mineralogie. Geologie und Paläontologie 3, 475–477.

Dong, W., Hu, Ch., 1994. The Late Miocene Cervidae from Hounao, Yushe Basin, Shanxi. Vertebrata PalAsiatica 32, 209–227.

Flerov, K.K., 1952. Musk deer and deer, Fauna of the USSR. Mammals. I (2) USSR Academy of Sciences Press, Moscow, Leningrad, [in Russian].

Flynn, L.J., Tedford, R.H., Qiu, Z., 1991. Enrichment and stability in the Pliocene mammalian fauna of North China. Paleobiology 17, 246–265.

Geist, V., 1999. Deer of the World: their evolution, behaviour, and ecology. Swan Hill Press, Shrewsbury.

Gentry, A.W., Rössner, G.E., Heizmann, E.P.J., 1999. Suborder Ruminantia. In: Rössner, G.E., Heissig, K. (Eds.), The Miocene land mammals of Europe. Verlag Dr. Friedrich Pfeil, München, pp. 225–258.

Gilbert, C., Ropiquet, A., Hassanin, A., 2006. Mitochondrial and nuclear phylogenies of Cervidae (Mammalia, Ruminantia): systematics, morphology, and biogeography. Molecular Phylogenetics and Evolution 40, 101–117.

Gould, S.J., 1973. Positive allometry of antlers in the ‘‘Irish Elk’’, *Megaloceros giganteus*. Nature 244, 375–376.

Heintz, E., 1970. Les cervidés villafranchiens de France et d’Espagne. Mémoires du Muséum national d’histoire naturelle, série 5. Sciences de la terre 22, 1–303.

Hu, Ch., Qi, T., 1978. Gongwangling Pleistocene mammalian fauna of Lantian, Shaanxi. Palaeontologia Sinica 155, 1–64 [new series C].

Hughes, S., Hayden, Th.J., Douady, Ch.J., Tougard, Ch., Germonpré, M., Stuart, A., Lbova, L., Garden, R.F., Hänni, C., Say, L., 2006. Molecular phylogeny of the extinct giant deer, *Megaloceros giganteus*. Molecular Phylogenetics and Evolution 40, 285–291.

ICZN (International Commission of Zoological Nomenclature), 1989. Opinion 1566: *Megaloceros* Brookes, 1829 (Mammalia, Artiodactyla): original spelling emended. Bulletin of Zoological Nomenclature 46, 219–220.

Kahlke, H.D., 1965. Die Cerviden-Reste aus den Tonen von Voigstedt in Thüringen. Paläontologische Abhandlungen A 2, 379–426.

Kahlke, H.D., 1969. Die Cerviden-Reste aus den Kiesen von Süssenborn bei Weimar. Paläontologische Abhandlungen A 3, 547–610.

Kahlke, H.D., 1971. Family Cervidae Gray, 1821. In: Nikiforova, K.V. (Ed.), The Pleistocene of Tiraspol. Shtiinza, Kishinev, [in Russian], pp. 137–156.

Kahlke, H.D., 1975. Die Cerviden-Reste aus den Travertinen von Weimar-Ehringsdorf. Paläontologische Abhandlungen 23, 201–246.

Kahlke, H.D., 1997. Die Cerviden-Reste aus dem Unterpleistozän von Untermassfeld. In: Kahlke, R.D. (Ed.), Das Pleistozän von Untermassfeld bei Meiningen (Thüringen). Verlag Dr. Rudolf Habelt, Bonn, pp. 181–275.

Kahlke, H.D., Hu, Ch., 1957. On the distribution of *Megaceros* in China. Vertebrata PalAsiatica 1, 273–283.

Kahlke, R.D., 1999. The history of the origin, evolution and dispersal of the Late Pleistocene *Mammuthus - Coelodonta* faunal complex in Eurasia (large mammals). Mammoth site of Hot Springs, South Dakota Inc.

Khomenko, I., 1913. Meotian fauna of v. Tarakliya of Bendery district. Annuaire géologique et minéralogique de la Russie 15, 107–132 [in Russian].

Korotkevitsch, E.L., 1970. Late Neogene deer of the Black Sea coast area. Naukova Dumka, Kiev, [in Russian].

Korotkevitsch, E.L., 1988. A history of the *Hipparion* fauna of Eastern Europe. Naukova Dumka, Kiev, [in Russian].

Kuehn, R., Ludt, Ch.J., Schroeder, W., Rottmann, O., 2005. Molecular phylogeny of *Megaloceros giganteus* - the giant deer or just a giant red deer? Zoological Sciences 22, 1031–1044.

Li, M., Tamate, H.B., Wei, F., Wang, X., Masuda, R., Sheng, H., Ohtaishi, N., 2003. Phylogenetic relationships among deer in China derived from mitochondrial DNA cytochrome b sequences. Acta Theriologica 48, 207–219.

Lister, A.M., 1987. *Megaceros* or *Megaloceros*? The nomenclature of the giant deer. Quaternary Newsletter 52, 14–16.

Lister, A.M., 1994. The evolution of the giant deer. *Megaloceros giganteus* (Blumenbach). Zoological Journal of the Linnean Society 112, 65–100.

Lister, A.M., Edwards, C.J., Nock, D.A.W., Bunce, M., van Pijlen, I.A., Bradley, D.G., Thomas, M.G., Barnes, I., 2005. The phylogenetic position of the ''giant deer'' *Megaloceros giganteus*. Nature 438, 850–853.

Matthew, W.D., 1929. Reclassification of the Artiodactyl Families. Bulletin of Geological Society of America 40, 403–408.

McKenna, M.C., Bell, S.K., 1997. Classification of mammals above the species level. Columbia University Press, N.Y..

Otsuka, H., Shikama, T., 1977. Studies on fossil deer of the Takao collection (Pleistocene deer fauna in the Seto Inland Sea, West Japan - part 1). Bulletin of the National Science Museum 3, 9–40.

Petronio, C., Krakhmalnaya, T., Bellucci, L., Di Stefano, G., 2007. Remarks on some Eurasian pliocervines: characteristics, evolution, and relationships with the tribe Cervini. Geobios 40, 113–130.

Pfeiffer, T., 1999. Die Stellung von *Dama* (Cervidae, Mammalia) im System plesiometacarpaler Hirsche des Pleistozäns. Phylogenetische Rekonstruktion - Metrische Analyse. Courier Forschungsinstitut Senckenberg 211, 1–218.

Pfeiffer, T., 2002. The first complete skeleton of *Megaloceros verticornis* (Dawkins, 1868) (Cervidae, Mammalia) from Bilshausen (Lower Saxony, Germany): description and phylogenetic implications. Mitteilungen aus dem Museum für Naturkunde in Berlin. Geowissenschaftliche 5, 289–308.

Pitra, C., Fickel, J., Meijaard, E., Groves, C., 2004. Evolution and phylogeny of Old World deer. Molecular Phylogenetic and Evolution 33, 880–895.

Radulesco, C., Samson, P., 1967. Sur un nouveau cerf mégacérin du Pléistocène moyen de la dépression de Brasov (Roumanie). Geologica Romana 6, 317–344.

Shikama, T., Tsugawa, S., 1962. Megacerid remains from Gunma Prefecture, Japan. Bulletin of the National Science Museum 6, 1–13.

Teilhard de Chardin, P., 1936. Fossil mammals from Locality 9 of Choukoutien. Palaeontologia Sinica 5–70 [series C 7].

Teilhard de Chardin, P., Pei, P.A., 1941. The fossil mammals from locality 13 of Choukoutien. Palaeontologia Sinica 1–119 [new series C 11].

Van der Made, J., 2006. The evolution and biogeography of the Pleistocene giant deer *Megaloceros giganteus* (Cervidae, Mammalia). Courier Forschungsinstitut Senckenberg 256, 117–129.

Van der Made, J., Tong, H.W., 2008. Phylogeny of the giant deer with palmate brow tines *Megaloceros* from West and *Sinomegaceros* from East Eurasia. Quaternary International 179, 135–162.

Viret, J., 1961. Artiodactyla. In: Piveteau, J. (Ed.), Traité de Paléontologie 6 (1). Masson et Cie, Paris, pp. 887–1084.

Vislobokova, I.A., 1979. A new deer from the Pliocene of Mongolia. Transactions of the Joint Soviet-Mongolian Paleontological Expedition 8, 31–38 [in Russian].

Vislobokova, I.A., 1981. On the early evolution of megacerines. Paleontological Zhurnal 4, 105–117 [in Russian].

Vislobokova, I.A., 1983. The fossil deer of Mongolia. Nauka, Moscow, [in Russian, English summary].

Vislobokova, I.A., 1988. Family Cervidae Gray, 1821. In: Nikiforova, K.V., Vangengeim, E.A. (Eds.), Biostratigraphy of the Late Pliocene-Early Pleistocene of Tadzhikistan. Nauka, Moscow, [in Russian], pp. 72–98.

Vislobokova, I.A., 1990. The fossil deer of Eurasia. Nauka, Moscow, [in Russian, English summary].

Vislobokova, I.A., in press. First fossil remains of *Chleuastochoerus* (Suidae, Artiodactyla) in the territory of Russia. Paleontological Zhurnal.

Vislobokova, I.A., Hu, Ch., 1990. On the evolution of megacerines. Vertebrata PalAsiatica 28, 150–158.

Vislobokova, I.A., Lavrov, A.V., 2009. The most ancient moschids of the genera Moschus in the territory of Russia and their significance to clarify the evolution and relationships of the family Moschidae. Paleontological Journal 43, 326–338.

Young, C.C., 1932. On the Artiodactyla from the *Sinanthropus* Site at Choukoutien. Palaeontologia Sinica 1–159 [series C 8].

Zdansky, O., 1925. Fossile Hirsche Chinas. Palaeontologia Sinica 1–93 [series C 2].

Zdansky, O., 1928. Die Säugetiere der Quartärfauna von Choukoutien. Palaeontologia Sinica 1–146 [series C 5].